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The effect of kinship on helping in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*)

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SUMMARY

It has previously been argued that the feeding of nestlings by non-parental birds may simply be an unselected consequence of delayed dispersal in cooperative breeding birds in which individuals follow simple rules such as 'feed any begging mouth in my natal territory'. However, in the cooperative breeding Seychelles warblers (*Acrocephalus sechellensis*), helpers are more likely to help feed full siblings (both parents still alive) than half-siblings (one parent died), and do not help at all when the young are unrelated (both parents replaced). Helpers, helping both full siblings and half-siblings reduced their helping effort (food provisioning and period of helping) significantly when rearing young of lesser relatedness. These behaviours suggest that helping has been selected for in the context of promoting an individual's indirect fitness, and that it is not simply a by-product of 'provisioning behaviour'. The mechanism by which kin discrimination in helping is achieved appears to be associative learning; birds more often became helpers at nests belonging to related individuals who fed them (as a parent or a helper) when they were nestlings than at nests of related breeders who had not fed them in the nest.

1. INTRODUCTION

Cooperative breeding is a reproductive system in which adults in addition to parents provide care (usually food provisioning) in the rearing of young. The aid-givers may be non-breeding adults, in which case they are usually called helpers, or cobreeders who share reproduction with other group members. The 'decision' of a helper to help should be viewed as the result of two complementary processes: the decision to stay in the natal unit, and the decision to help. In many species, the indirect genetic benefit from helping is far less than the potential direct genetic gain from breeding if a territory and mate could be obtained (Brown 1978). One explanation for helping could be direct fitness gains through increased survival or territory inheritance (see, for example, Reyer 1984). However, future direct fitness gains of the helping strategy are not sufficient to account for cooperative breeding. Helping behaviour could also be explained by reciprocal altruism and kin selection. In reciprocity, the helped offspring will help their previous helpers, who have become breeders, so that the original helpers recoup the helping investment. Indirect fitness gains of the helping strategy might be important too (Brown 1980; Emlen & Wrege 1988). The indirect gain to a helper is the product of two terms: (i) the increase in the number of young successfully produced by the breeding pair as a result of the activities of the helper;

and (ii) the coefficient of relatedness between helper and the young it helps to rear. Cooperative breeding can be kin selected if helpers either increase parents' present reproductive success or increase parents' survival, by lessening their work, and hence increasing their future reproductive success. However, the idea that helping behaviour has been selected for in the context of promoting an individual's inclusive fitness has been criticized. It could simply be no more than a by-product of 'provisioning behaviour', whereby individuals follow simple rules such as 'feed any begging mouth in my natal territory' (Brown & Brown 1980; Rabenold 1985; Jamieson 1986, 1989; Jamieson & Craig 1987).

In this paper I address these criticisms based on analyses of helping in the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*), a rare endemic known only from the Seychelles Islands. Until 1988, it occurred only on Cousin Island (29 ha), but additional breeding populations were successfully established on the islands of Aride (68 ha) and Cousine (26 ha) in September 1988 and June 1990, respectively (Komdeur 1994a). The most common clutch size is one (87.0%, $n = 169$). First year mortality is high, especially after fledging: 16.5% of nestlings die before fledging, 45.0% before independence, and 68.1% before one year of age ($n = 91$). However, adult survivorship is high (the probability of surviving to the next year, starting at age 1 year old, is 83.5% (Komdeur 1991)). Although Seychelles warblers can breed successfully in their first year, some individuals remain on their natal territories and do not breed for several years, sometimes throughout their life. On

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Cousin Island, the average group size is 2.9 birds (range 2–12). The basic unit is the breeding pair, which remain together in the same territory as long as both birds survive, sometimes as long as 9 years. Virtually all offspring that fail to become breeders remain on their natal territory, from which they foray into the surrounding area searching for breeding vacancies. Helpers aid in territory defence, predator mobbing, nest building, incubation (females only), and feeding of dependent young which are probably not genetically their own offspring (Komdeur 1994*b*). However, extra-pair copulations, joint nesting (where more than one female lay eggs in the same nest) and egg removal occur (Komdeur 1991, 1994*b*). Cooperative breeding is promoted not only by habitat saturation, but also by competition for higher quality territories (Komdeur 1992, 1993). Young birds were more likely to help and parents and young were more likely to survive on good quality territories (Komdeur 1992). After controlling for territory quality, significantly more females than males were helpers. The probability of helping rose to reach a plateau with increasing age. In both female and male non-breeders, the probability of helping was the same during the second and third year of age (Komdeur 1991). Removal experiments showed that the presence of helpers on good quality territories improved the reproductive success of their parents, due to helping behaviour (Komdeur 1994*b*). Helpers which did not care for the young in the nest never began acting as helpers after the young fledged ($n = 161$).

This study was designed to answer two questions. First, is kin selection important for the evolution and maintenance of helping behaviour in the Seychelles warbler, or do helpers ‘automatically’ feed any nestlings within their own group? Natural variation in kin relationships within Seychelles warbler groups provided an excellent opportunity for investigating the influence of kinship on helping behaviour. Second, if kinship is important, what is the mechanism by which kin discrimination in helping is achieved? This could be associative learning or direct kinship assessment. In associative learning, birds could more often become helpers at nests belonging to breeders who fed them (as a parent or a helper) when they were nestlings than at nests of related breeders who had not fed them in the nest.

2. MATERIAL AND METHODS

(a) Data collection

The entire population of Seychelles warblers on Cousin Island (115–123 groups, 310–400 birds) was under continuous study between December 1985 and June 1991. Observations were made on individually colour-ringed birds. All territories were checked fortnightly for active nests and presence of colour-ringed birds. All nests were checked for clutch size. Observations of food provisioning and the presence of birds closer than 0.5 m to nest were made for 3 h comprising three sessions of 1 h equally spaced over the day: 06h30–10h30, 10h30–14h30, and 14h30–18h30. Feeding observations started in the second week after hatching and were repeated every 3 weeks until the offspring died or

reached independence. For each half-minute it was noted whether or not each bird was taking part in each of the above-mentioned categories. The effect of kinship on helping was based on observations of individuals feeding nestlings in the second week after hatching, because of high post-fledging mortality.

(b) Territory quality

Territory quality, which was not determined by the presence of nest sites and nest predators (Komdeur 1991, 1994*b*), was measured in terms of insect prey available. As the warblers are insectivorous, taking 98% of their insect food from leaves (Komdeur 1991), the quality of a territory depends on insect prey available and amount of foliage. Details of the method of measuring territory quality (tq) are presented elsewhere (Komdeur 1991, 1994*b*). Territories were divided into three categories: low ($tq = 0–15$), medium ($tq = 15–30$) and high quality ($tq = 30–45$).

(c) Kinship assessment

In this paper, I define a helper as ‘an individual that contributes physically, but not genetically, to young being reared’. Despite the complications of cobreeding in the Seychelles warbler, most territories contained just one breeding pair, together with some of their previous offspring which acted as helpers. The commonest clutch size is one, and was probably laid in almost all cases by the dominant female. Normally, females laid very early in the morning, and it was assumed that, if only one female was on the nest, the new egg was laid by that particular female. When only one egg was present in groups of 2–4 individually known females ($n = 17$), this egg was always laid by the mother (i.e. only she was on the nest 30 min before sunrise when the first egg was laid and no further eggs were laid). Kinship calculations were based on genealogical data. To identify genetic ties within social units, with as little effect as possible caused by cobreeding, only territories with nests containing one egg were considered, and the assumption was made that the behavioural parents (breeders) were the genetic parents of the young they reared, and that no breeding status was achieved by the helper within the bird’s original group.

(d) Kinship and helping behaviour

Only those birds which had an opportunity to help were included in the analyses, i.e. those with a nest with young present in their natal territories. Each of these potential helpers was counted once for each pair it could have helped. Three relatedness categories of potential helpers with nestlings were distinguished: full sibs (both parents of the potential helper still alive), half-sibs (one parent died), and unrelated birds (both their parents have been replaced by new breeders). The effects of age and gender of birds in kin discrimination were controlled for by considering two- and three-year-old helpers only, separated by sex. However, territory quality could also affect helping decisions. More helping of full sibs on good quality territories may occur, because on these territories young birds were more likely to help and parents more likely to survive, and hence produce more full sibs for young to help. Territory quality effects were controlled for by considering helping decisions on medium- and high-quality territories separately. Not enough data were available to include helping decisions on low-quality territories.

Another way to test for kin discrimination is to ask whether

Table 1. Influence of relatedness of nestlings with potential helpers on percentage of Seychelles warblers helping on (a) medium- and (b) high-quality territories

(Each bird was 2 or 3 years of age and was counted once for each pair it could have helped in a breeding season. Only nests with single pulli hatched from clutches of one egg are included (n = helper seasons, 1986–1990).)

(a) Medium-quality territory

relatedness category ^a	sex of potential helper					
	males		females		total	
	percentage helping	n	percentage helping	n	percentage helping	n
full sibs ($r \approx 0.50$)	66.7	12	81.8	11	73.9	23
half-sibs ($r \approx 0.25$)	44.4	9	40.0	5	42.9	14
unrelated ($r \approx 0.0$)	0.0	5	0.0	3	0.0	8
G-test (d.f. = 2) ^b	8.25*		8.70*		18.43**	

(b) High-quality territory

relatedness category ^a	sex of potential helper					
	male		female		total	
	percentage helping	n	percentage helping	n	percentage helping	n
Full sibs ($r \approx 0.50$)	60.0	15	80.0	15	73.3	30
half-sibs ($r \approx 0.25$)	36.4	11	66.7	6	47.1	17
unrelated ($r \approx 0.0$)	0.0	6	0.0	4	0.0	10
G-test (d.f. = 2) ^b	8.62*		10.02*		20.70**	

^aEstimated minimum relatedness between potential helper and nestlings.

^bG-tests of independence; * $p < 0.025$; ** $p < 0.001$.

help was always directed to the more closely related of two potential sets of recipients (Emlen & Wrege 1988). Sometimes young warblers had the simultaneous choice to help at two different nests on their natal territory: that of their parents, and that of an unrelated female mated with their polygynous father.

I also considered the following question: if a helper helps, does kinship influence how much it helps? However, the death of either the father or the mother could also affect helping efforts. Data were available on feeding efforts of the same helpers to full sibs and half- or unrelated sibs in the year before and in the year after the death of the father, or both parents, respectively. Not enough data were available to compare helping efforts to young before and after the death of the mother (father still alive). The internal control used (comparing feeding rates of helpers, separated by sex, on the same territory in the year before and in the year after the father or both parents have died) is an explicit matched-pairs control for territory quality, age and experience of the helper. All helpers in this matched-pairs test helped full sibs in year x and half-sibs in year $x + 1$. As helping effort to full sibs increases with helper age (Komdeur 1991), the assumption could be made that a decrease in helping effort to half-sibs in the next year would be even more significant if helping effort was controlled for helper age.

3. RESULTS

(a) The effect of kinship on helping

Both males and females on medium- and high-quality territories more often became helpers to

nestlings which were close relatives. Young males and females who remained on their natal territory were more likely to help feed the nestlings if they were full sibs than if they were half-sibs, and they did not help at all if they were unrelated (table 1).

Further strong support for the influence of kinship on helping was also provided by the following observations. A female helper that fed full sibs during two consecutive breeding seasons did not feed half-sibs derived from her mother and an intruding male (who expelled her father from the territory) during two breeding seasons, but resumed feeding full sibs when her father regained the territory after the death of the intruding male. A female helper that fed full sibs during three consecutive breeding seasons did not help when an unrelated pair arrived and bred on the territory during two breeding seasons when her parents were translocated to Aride Island. A male helper that fed full sibs during two consecutive breeding seasons did not help when an unrelated pair arrived and bred on the territory during three breeding seasons when his parents were translocated to Cousine Island.

In this study, all young warblers ($n = 10$) with chances to help simultaneously at two different nests in polygynous groups on their natal territory helped only at the one containing more closely related nestlings (binomial-test, $p = 0.002$); each aided its parents (full sibs) in preference to its father paired with an unrelated female (half-sibs). Also, after fledging, the helpers selected only the young of their parents to feed, even

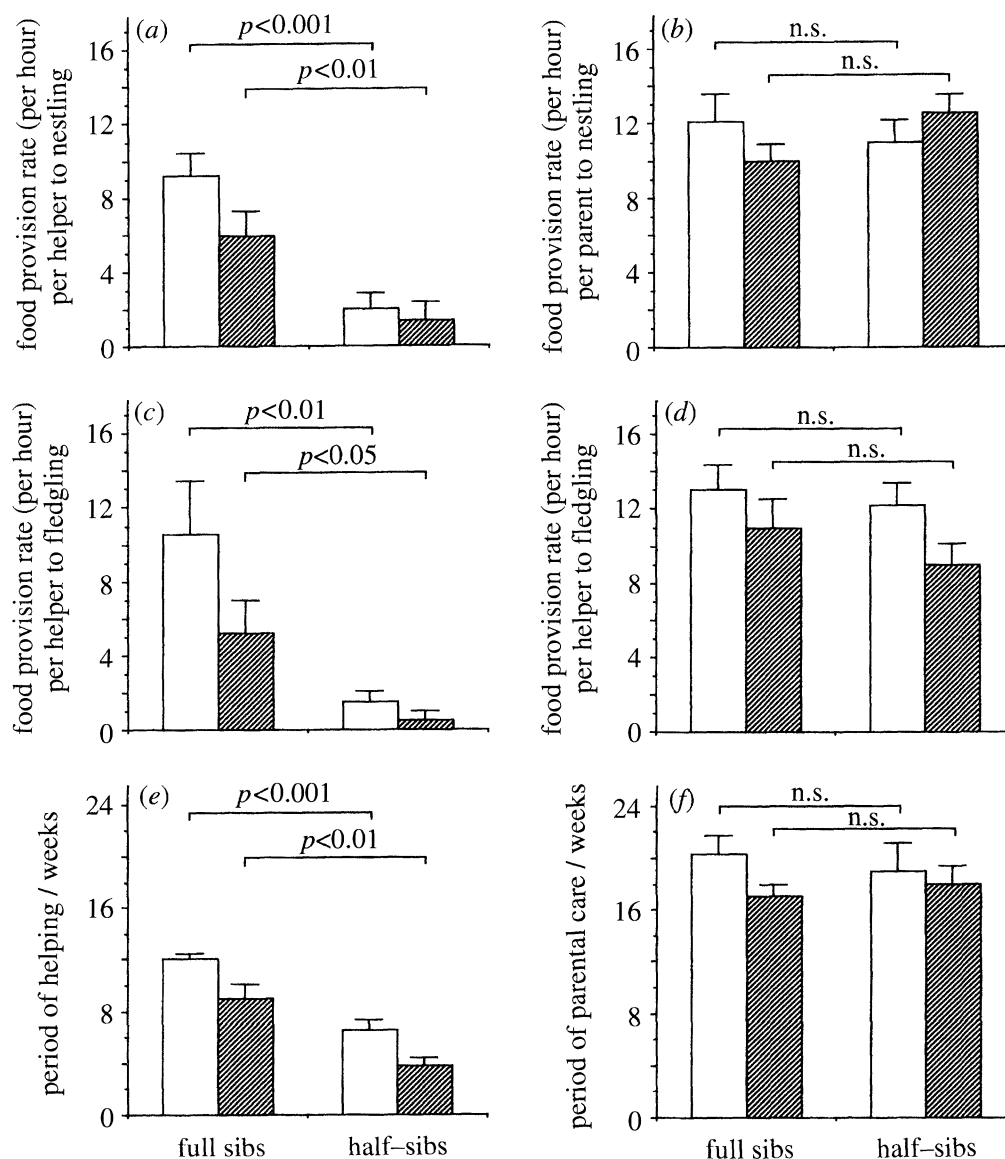


Figure 1. Effect of kinship on helping effort by female and male helpers alongside mean helping effort per parent of the young, measured as food provision rate to two-week-old nestlings ((a) and (b), respectively) and five-week-old fledglings ((c) and (d), respectively), and length of period of helping ((e) and (f), respectively), in the year before (full sibs) and after the death of the father (mother alive, half-sibs). In (a), (c) and (e), results show females ($n = 6$, unshaded columns) and males ($n = 4$, shaded columns); in (b), (d) and (f), results are with female helpers (unshaded columns) and with male helpers (shaded columns). All helpers helped feed full and half-sibs, and were between 2 and 3 years of age. Only nests with single pulli hatched from clutches of one egg are included. All young survived to independence. Means and standard errors are shown. Values of P determined by one-tailed paired-sample t -test.

though both young were begging for food simultaneously.

(b) *The effect of kinship on helping effort*

The feeding rates of helpers to full sibs were compared with those of the same helpers feeding half-sibs. Helpers reduced their effort significantly when rearing young of lesser relatedness than full sibs (figure 1a, c). Care by male and female helpers to full sibs lasted for a significantly longer period than care by the same helpers to half-sibs (figure 1e). Helpers did not feed half-sibs less and over a shorter period because they were getting better care from the parents; in all cases, parents worked as hard (figure 1b, d) and as long (figure 1f) for the helpers' full sibs as for their half-sibs.

(c) *Mechanism of kin discrimination*

The mechanism by which kin discrimination in helping is achieved appears to be associative learning. The observed pattern of helping better matches that expected from a mechanism based on association than from kinship alone; birds more often became helpers at nests belonging to individuals who fed them when they were nestlings (table 2). When the potential helper had the simultaneous choice of feeding full sibs or nestlings with the same degree of relatedness ($r = 0.5$) from an incestuous breeding pair, consisting of a full brother and sister who had not fed the potential helper in the nest, it only fed the full sibs. When the potential helper had the simultaneous option of feeding nestlings from a brother-sister combination ($r = 0.5$), who had not fed

Table 2. Influence of relatedness of nestlings with potential helpers (2 or 3 years of age) and past association between breeders and potential helpers on helping decisions in the Seychelles warbler

(Only nests with single pulli hatched from clutches of one egg are included (n = helper seasons).)

breeder combination	number of breeders that fed potential helper in the nest	relatedness nestlings	percentage helping	n
parents	both	0.5	100	9
brother \times sister (binomial test)	neither	0.5	0 (p = 0.0039)	
brother \times sister	neither	0.5	0	12
parent \times step-parent (binomial test)	one	0.25	100 (p = 0.0005)	
parents	both	0.5	100	4
sister \times unrelated (binomial test)	one	0.25	100 (p = 0.1250)	

the potential helper in the nest, or feeding half-sibs from a parent–step-parent combination, it only aided the parent–step-parent combination even though, in this case, their young were less-related siblings. When the potential helper had the simultaneous choice of feeding full sibs from its parents or nestlings from a sister (r = 0.25), who was a helper when the potential helper was an offspring, it provided help at both nests.

4. DISCUSSION

The data on the context in which helping occurs suggest that helping behaviour in the Seychelles warbler has been selected for, and that it is not a simple behavioural response to the presence of begging nestlings. However, an alternative explanation could be the ‘evil step-parent hypothesis’: aggression from step-parents may prevent potential helpers from gaining access to the nest and becoming helpers (Jamieson & Craig 1990). The data presented here were not influenced by the behaviour of step-parents. In all the cases with half-sibs and unrelated nestlings (n = 49), the step-parents did not prevent potential helpers from gaining access to the nest and becoming helpers. I saw no evidence that potential helpers who were simultaneously present at the nest with the step-parent(s) were ever displaced by the step-parent(s) (n = 56). This strengthens the interpretation that the provision response is a kin-selected adaptation rather than a non-adaptive by-product. Good evidence for a role of kin selection in directing the target of helping behaviour is also shown for the bell miner (*Manorina melanophrys*) (Clarke 1984), the Galápagos mockingbird (*Nesominus parvulus*) (Curry & Grant 1990), the white-fronted bee-eater (*Merops bullockoides*) (Emlen 1990) and the brown hyena (*Hyaena brunnea*) (Owens & Owens 1984). In these species, individuals preferentially aid relatives over non-relatives, when both are simultaneously available to be helped.

Several lines of evidence suggest that Seychelles warblers follow a rule of thumb for helping that is based on the identity of the breeders, rather than the identity of nestlings. The observed pattern of helping better matches that expected from the rule ‘help anyone who fed me when I was a nestling’ than ‘help

my parents’. If helping is based on the identity of breeders then this would require more discriminatory ability than other rules helpers might follow, such as ‘feed at any nest within my natal territory’. Theoretically, a mechanism for discriminatory helping based on social learning could be vulnerable to deception: unrelated birds could act as helpers to deceive nestlings into recognizing them as relatives, to which the nestlings would then direct help when they become older. This was probably the case in the Galápagos mockingbird, where unrelated helpers did occur, and clear evidence existed for the associative learning hypothesis (Curry 1988). In the Seychelles warbler, unrelated helpers did not exist so this possibility did not occur.

The mechanisms by which kin discrimination in helping is achieved could be investigated through cross-fostering experiments in which eggs are transferred to ‘foster’ nests and hatched by unrelated breeders. Young hatched by the true parents will serve as a control. Do these young become helpers at nests belonging to unrelated breeders who fed them when they were nestlings (associative learning) or at nests to related breeders?

The kin-selected adaptation of provisioning response by the Seychelles warbler suggests that helping behaviour has been selected for in the context of promoting an individual’s indirect fitness (Brown 1980; Emlen & Wrege 1988). Indirect genetic benefits to helpers and direct benefits to parents or helped nestling do exist. Removal experiments in the Seychelles warbler have revealed that breeding pairs with one helper produce significantly more yearlings per year than do the same breeding pairs after removal of the helper (0.88 and 0.17 yearlings, respectively (Komdeur 1994*b*). As the costs of helping are negligible, and helping does not influence breeder survival, the increased reproductive success is entirely the result of helping (Komdeur 1994*b*). Assuming that no breeding status was achieved by the helper within its original group, and that it was the only helper present, a one-year-old warbler could produce more offspring over its lifetime by remaining in its natal territory as a helper feeding full sibs or half-sibs (thereby gaining 0.71 and 0.36 yearling equivalents annually, respectively) than

it could by dispersing and breeding immediately (with an average production of 0.17 yearlings annually) (Komdeur 1994*b*). However, breeding benefits are always greater than helping benefits from feeding unrelated young. By preferentially choosing to aid close, as opposed to distant, kin, a Seychelles warbler can gain more in indirect fitness as a helper than it could in direct fitness as a breeder. Therefore feeding dependent offspring within the territory is an adaptive consequence of its effect on the fitness of the helper or its relatives, and not simply a by-product of living in groups.

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